It is a common observation that at room temperature a Venus' flytrap (Dionaea) leaf will normally not respond if its trigger hair is touched only once but that it will snap shut if a second stimulus is delivered either to the same hair or to any other hair of the trap. It is often stated that the trap "remembers" the first stimulus.

Sir John Scott Burdon-Sanderson first described this phenomenon in 1876 and it has been described by many other workers since then. Unfortunately, despite their extent and elegance, Burdon-Sanderson's experiments are given only superficial treatment in Lloyd's extensive monograph on carnivorous plants so his work has not received the attention that it deserves. It is by far the most accurate description of the movements of Dionaea ever published.

Whilc it is true that the leaf will snap shut after a second touch if the second touch is delivered within about 20 or 40 seconds of the first, stimulation at greater intervals reveals a more complex story. The movement in response to the second touch is not a complete closure and the trap will also respond to a third touch. At a sufficiently long interval the trap will respond to each of a series of touches after the first in a pattern which is best illustrated with Burdon-Sanderson's own data.

Figures 1 and 2 illustrate apparatus similar to that which Burdon-Sanderson used in this experiment. A stylus is attached to a device which fits between the trap lobes so that it swings upward as the trap closes and makes a mark on a smoked drum as the drum rotates. This results in the tracing of the position of the trap lobes on the drum as a function of the time and produces a graph such as that in Figure 3 where time is on the horizontal axis and trap movement on the vertical axis. In the particular graph illustrated the stimuli were delivered at 1 minute intervals. It can be clearly seen that the trigger hair had to be touched six times to close this trap, that there was no response to the first touch (1), that the trap responds to each successive touch, ${ }^{*}$ that the response to each successive touch was greater than to the one preceeding it, and that the movements in response to each touch sum up to close the trap. Animal tissues often produce similar responses to a series of evenly spaced stimuli and physiologists have used the word facilitation to describe processes by which response to a stimulus is increased by a previous stimulus. The "memory" of the Venus' flytrap can more accurately be called facilitation.

If stimulation at one minute intervals reveals this complex pattern, what happens at even larger intervals? Burdon-Sanderson published other data showing that touches spaced at 2 minute intervals did not cause the trap he was observing to move until the trigger hair had been touched 10 times and that it did not fully close until the hair was touched 27 times. In 1916 William H. Brown did experiments similar to those of Burdon-Sanderson. He extended the observations to very long intervals and made a graph of the average number of touches needed to close a trap at each interval. The graph is shown in Figure 4. It gives the results of a series of experiments

* Burdon-Sanderson observed that the movement occurs one second after the action potential sweeps over the trap and about two seconds after the hair is touched. Others have confirmed the first of these observations. For more information on the Dionaea action potential see the excellent papers by Sibaoka, 1966, Symposium for Quantitative Biology 20, 49 and Benolken and Jacobson, 1970, J. Gen. Physiol. 56, 64 .

Fig. 1.


Fig. 3.
1 min.

Fig. 1.* Hinged device which fits inside the two trap lobes of a Dionaea leaf. Fig. 2. The hinged device (Fig. 1) in operation. The trap base is placed on a glass rod which is attached to the screw clamp that supports the stationary jaw of the hinged device. The smoked drum rotates at a constant rate and is marked, as it turns, by the stylus attached to the hinged device.
Fig. 3.* A graph traced by the stylus on the surface of a smoked drum such as that in Fig. 2. The trigger hair was pushed with a camel's hair brush at each of the numbered marks along the baseline. Note that the response occurs just after the stimulus and that the response to every stimulus is much greater than the response to the stimulus before it.

* Negative photographs of original drawings in Burdon-Sanderson and Page, Proc.
Roy. Soc. $25,411(1876)$.

Fig. 4. The average number of times the trigger hair must be touched to close a trap plotted against the length of time between touches applied to the hair. The more frequently the trigger hair is touched the fewer the number of touches required to close it. The bars represent one standard deviation. Plotted from data in Brown, Amer. J. Bot. 3, 68 (1916).
similar to that in Figure 3. The number of stimuli required to close the trap is plotted against the interval between stimuli. The data from Figure 3 could be plotted on the graph at ( 1,6 ). They are somewhat above the average number of stimuli observed by Brown to be sufficient to close the trap at this interval. This is most likely due to the fact that Brown's traps did not have to lift the hinged device and stylus and thus less work was required to move the lobes enough to close them. The data in Figure 4 and Brown's other data indicate that behavior similar to that observed by Burdon-Sanderson at one and two minute intervals can be observed at stimulation intervals of up to 20 minutes.

Of course no insect is going to patiently sit and stimulate a trap at 20 minute intervals for the seven hours it would take to get caught. Only the first two touches are likely to be important in the initial capturing movements in nature, where it may be hypothesized that the lack of response to the first touch benefits the plant by preventing accidental closure by windblown sand, raindrops, etc. As it struggles inside, the insect delivers to the hair many closely spaced stimuli which aid in tightening the trap* but nowhere would one expect to see stimuli applied at intervals similar to those Brown used. What do such experiments demonstrate then? The response to stimuli delivered at long intervals gives us a much more accurate description of the trap movements and allows them to be compared to movements in other plants and animals. The data may help in elucidating the mechanism of trap closure. It should also be of interest to evolutionary botanists since a similar phenomenon exists in Drosera where more than two responses are normally involved in tentacle movement.*

* Burdon-Sanderson proved this by attaching weights to the stylus shown in Figure 1. This forced the lobes open but further stimulation closed them again, lifting the weights in the process.
** The movements of Drosera and their similarity to those of Dionaea are discussed in 1972 in my papers with Barbard Pickard, (Planta 103, 193).


## SOME FIELD OBSERVATIONS OF DARLINGTONIA AND PINGUICULA

by Robert R. Ziemer
In mid-February I visited a number of field sites in the Smith River drainage of northwestern California near Gasquet where Darlingtonia (Chrysamphora) californica and Pinguicula vulgaris grow extensively. All of the sites I located were confined to areas underlain by Mesozoic ultrabasic intrusive rocks. I could find no CP sites on the metavolcanic rocks which surround the ultrabasics. Whether parent material is a limiting condition in this region would require a more detailed investigation.

The climate at Gasquet can be classed as Mediterranean--cool, wet winters with warm, dry summers. Rainfall averages 94 inches with less than 5\% falling from June through September. Winter temperatures are mild with a mean minimum January temperature of $35^{\circ} \mathrm{F}$. and the lowest observed temperature near $20^{\circ} \mathrm{F}$. The maximum mean July temperature is about $75^{\circ} \mathrm{F}$. with a maximum observed temperature near

